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Significance of functional and structural relationships in the soil and litter layer

BY

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INTRODUCTION

The question: « How operates a biocommunity ? », is the most difficult and at the same time the most fascinating question to be tackled by ecologists. In this paper it is dealt with through investigations of plant and animal populations in so called « pioneer-situations ». In future it is aimed to continue this research to study any changes in the interrelationships of species (plants as well as animals) during the development of such a biocommunity.

A number of pioneer species are able to produce populations with high densities, on behalf of their high reproductive capacity. At the same time these populations normally survive only for a limited period of time (a couple of years), in dependence on changes of abiotic factors in the environment. In our opinion no coherent research has been performed into the interrelationships of populations of different trophic levels in developing biocommunities. It is found that, in « pioneer situations » quite a number of species is involved and that only part of the species of plants and animals, under such conditions, occur in high densities. With respect to the areas which are studied (cf. VLIJM, 1973) it was concluded that:

1. In a coastal plain (Schiermonnikoog) the number of plant species (higher plants) is about 85 (cf. J. H. IETSWAART, unpublished student reports and v.d. MAAREL, 1971) whereas higher numbers of animals species occur e.g. Coleoptera 200 species (cf. LITTEL, unpublished results). Araneae, 40 species (cf. VAN WINGERDEN, unpublished results).

2. In a newly constructed polder (Lauwerzeepolder) during three years of investigations (1969-1972) the number of higher plants was 166 (cf. JOENJE, 1974), of beetles (Coleoptera): 69, of Araneae: 83 (cf. MEYER, 1974 and unpublished results.)

3. In areas around Amsterdam, prepared to be used for construction of living quarters and industries, by pumping sand on the old land, up till now 40 species of higher plants (cf. LIEM, 1974) 30 species of beetles (Coleoptera), and 70 species of spiders (Araneae) were found.

In this study, special attention was paid to the interrelationships of those species occurring in high densities in different trophic levels. The following report concerns only one of the study-areas, i.e. the coastal plain of Schiermonnikoog. Attention was paid to:

1. algae (unicellular and filamentous algae);
2. springtails (Collembola), especially *Hypogastrura viatica* Tullb. 1872 (Coll. Hypogastruridae);
3. spiders (Araneae), especially *Erigone arctica* (White) (Ar., Linyphiidae);
4. some other spider (Linyphiidae) and beetle (Coleoptera) species, which only briefly are mentioned.

The data mostly are derived from VAN DER KRAAN (1971, 1973 and unpublished results), VAN WINGERDEN (1973 and unpublished results), as well as unpublished students reports (LITTEL, POPPE) and results of students field courses (1970, '71, '72 and '73).

STUDY AREA AND METHODS

a. *Study area.*

The study area mainly consists of the lower parts of a coastal plain at Schiermonnikoog, one of the Dutch Frisian islands. This island is bordered by the Dutch Wadden Sea and the North Sea. The original situation in this coastal plain (1957) was a broad beach (up to 1 kilometer), with lower areas and dunes with a height up till 3 meters. The greater part of this area, about 3 square kilometer was cut off from direct influences of the North Sea, by the construction of a sanddike, originated in 1958. This dike was built up with the help of forces of sanddrift. Details are to be found in VAN DER KRAAN (1973) and VAN WINGERDEN (1973).

In subsequent years a layer of silt was deposited in the lower areas, mainly during winterflooding of the coastal plain, by water, coming either from the North Sea, through gaps in the sanddike, or from the Dutch Wadden Sea. Populations of plants (mainly algae, afterwards also higher plants) ands animals (especially Hypogastrura viatica and Erigone arctica) were founded then.

In this area direct and indirect relationships between some of the forementioned organisms were studied.

b. *Methods.*

The techniques used are manifold. Details can be found in the cited papers. They mainly consisted of: quadrat-sampling (stratified sampling), pitfall-techniques,

and Tullgren techniques. The problems were approached in an experimental way as well. Furthermore direct observations, especially on the behaviour of animals in the field, gave an important contribution to a better knowledge of the studied phenomena.

RESULTS

A. **Data on the species which were studied.**

1. Algae.

A dense mat of algae, both filamentous and unicellular species, is found in the lower parts of the coastal plain. This layer is about 2-3 mm thick. The filamentous algae mostly are of the genus *Rhizoclonium*; the unicellular algae belong to a number of different genera. The filamentous algae form in the period of March and May a dense layer. In between, as well as at the surface of this layer, unicellular algae are found (cf. VAN DER KRAAN and VREUGDENHIL, 1973).

During summer, the layer of algae is broken apart by the drying of the surface layer. Crevices occur then. These crevices provide shelter for some terrestrial organisms (e.g. Collembola and sometimes spiders (cf. VAN DER KRAAN, 1971, 1973 and VAN WINGERDEN, 1973).

2. Hypogastrura viatica, Tullb. 1872 (Collembola, Hypogastruridae).

Hypogastrura viatica is a species which occurs in very high densities (10.000, sometimes up to 200.000 specimens are found per square meter). It feeds especially on unicellular algae (cf. VAN DER KRAAN and VREUGDENHIL, 1973). The species survives through winter presumably in a subadult stage. reproduction starts in April. The old generation then decreases, so that in mid-June it is no longer present.

In this species, as in other Collembola, moulting occurs rather frequently. During summer it is clear that the individuals moult about once in a fortnight. During the moulting process, the animals prefer high humidities and are locomotory inactive (cf. JOOSSE, 1971 ; DE WITH and JOOSSE, 1971). A sequence of feeding and reproductive intermoulting periods has been demonstrated with other Collembolan species (JOOSSE, 1971, 1973). Evidence could be found that in *Hypogastrura viatica* the same phenomena occur (cf. VAN DER KRAAN-MINDERHOUD and HERDER-BROUWER, unpublished results). The level of the locomotory activity during the intermoult periods is highly dependent on weather conditions.

The pattern of distribution of the species is dependent on the period of the year, moulting processes, as well as daily weather conditions.

In spring, when the humidity at the surface level generally is high, the population of *Hypogastrura viatica* is dispersed all over the lower parts of the beach plain. They are actively feeding then, especially in the intermoult periods.

In summer and early autumn the pattern of distribution is clumped, in dependence of places with a high humidity. Especially during periods of

bright weather the population is found under plant structures or in crevices. During the moult the same pattern is found.

In winter and early spring, and occasionally during spells of rainy weather in summer, when the lower parts of the coastal plain are flooded, the population of *Hypogastrura viatica* is wind drifted on the water surface. After such a period the population is concentrated along driftlines and is found there in incredible numbers. When the water retreats afterwards, *Hypogastrura viatica* recolonizes the lower parts. The population is found then in frontiers, which sometimes continue to maintain for several days (cf. VAN DER KRAAN, 1971). In a stretch of one meter of such frontiers up to two millions of specimens can be found.

3. *Erigone arctica* (White) (Araneae, Linyphiidae).

Erigone arctica occurs in densities of tens to hundreds, up to 400 specimens, per square meter in the lower parts of the coastal plain. This species feeds especially on *Hypogastrura viatica*.

Two periods of reproduction have been demonstrated:

a. In April-May.
   Specimens, having survived through winter are reproducing then.

b. In August.
   Specimens from the new generation, developed from eggsacs produced in April-May have grown up and are reproducing. Juveniles, emerged from eggsacs deposited in this period grow to adult through autumn, and reproduce in the next year (April-May) (cf. VAN WINGERDEN, 1974).

During spring, summer and autumn, *Erigone arctica* lives mainly in the lower parts of the coastal plain. In winter it is found especially in vegetation patches consisting of *Agrostis stolonifera* L. and *Festuca rubra* L. *Erigone actica* can survive periods of total submersion by means of skin respiration (cf. HEYDEMANN, 1960).

Details on the dispersion, based on aeronautic behaviour, of this species, are to be found in VAN WINGERDEN and VUGTS, 1974.

B. Relationships between the species.

1. DIRECT RELATIONSHIPS.

Food relationships between unicellular algae — *Hypogastrura viatica* — *Erigone arctica* have been observed. It could be concluded that:

a. Hypogastrura viatica eats only the unicellular algae, while filamentous algae are not used as a food resource (cf. VAN DER KRAAN and VREUGDENHIL, 1973).

Only those unicellular algae, present at the very surface can be used as a food resource for the species, as it is not able to dig into the bottom. When, however, the algal substrate is disturbed by activities of burrowing animals, or, in another way, crevices occur, unicellular algae of the lower layers are made accessible as a food resource (cf. indirect relationships).

b. Carnivorous animals of the soil and litter layer of the lower areas of the coastal plain depend mainly on *Hypogastrura viatica* as a food resource. *Erigone actica* was demonstrated to be the most important predator of *Hypogastrura viatica* (cf. VAN WINGERDEN, 1973, and POPPE, unpublished results). Densities as well as survival (eventually also dispersion) of *Erigone arctica* seem to be dependent directly on the densities of the main prey. In experiments it could be shown that mature females of *Erigone arctica* in the reproductive period deposit one eggsac every four days, for which a number of 35-40 specimens of *Hypogastrura viatica* are needed (VAN WINGERDEN, 1973).

Other carnivorous animals e.g. *Stenus* spec. (Coleoptera, Staphylinidae) prey also on *Hypogastrura viatica* (unpublished results of LITTEL and POPPE). Other beetle species e.g. *Dyschirius* spec. (Coleoptera, Carabidae) and spider species e.g. *Oedothorax retusus* (Westring), *Perimones arenarius* (Emerton), *Centromerita bicolor* (Blackwall) (Araneae, Linyphiidae) seem to prey occasionally on *Hypogastrura viatica.* They live mostly within vegetations of *Agrostis stolonifera* and *Festuca rubra* and prey normally on other Collembolan species,especially *Isotoma viridis* (Bourlet) f. *riparia.*

2. INDIRECT RELATIONSHIPS.

A number of different indirect relationships between the species could be established.

As mentioned before the population of *Hypogastrura viatica,* during flooding is concentrated in driftlines. After flooding it recolonizes the lower parts, in frontiers, sometimes with a length of several hundreds of meters. Under such conditions *Hypogastrura viatica* eats itself out of its food, being dependent on unicellular algae, present at the very surface, as a food resource.

However, when this algal mat is damaged, due to the activities of burrowing animals viz. *Bledius spectabilis* (Coleoptera, Staphylinidae), *Heterocerus* spec. (Coleoptera, Heteroceridae) and *Enchythraeus* spec. (Annelida, Enchythraeïdae), algae from deeper layers are made accessible and thus can be used as a food-resource.

Thus, the activity of « other » animals is important in making food accessible for the population of *Hypogastrura viatica.*

Furthermore the burrowing activities of these « other » animals provide shelter, and patches with high humidities for *Hypogastrura viatica* which are especially important during the moulting process.

During periods in which *Hypogastrura viatica* is feeding at the surface of the algal mat, *Erigone arctica* lives in excess of food. This occurs especially during early spring. After winterflooding the substrate is smoothed, and populations of filamentous and unicellular algae are building up, whereas species as *Bledius* spec. and *Heterocerus* spec. are not yet active in burrowing.

Later in the year (June, July, August), several species are active in burrowing. Crevices occur, in which *Hypogastrura viatica* can retreat for different activities (feeding, shelter or moult). Then *Erigone actica* is in a shortage of food, as this becomes inaccessible. This results in a decrease in egg-production and a lower natality in the second reproductive period of *Ergione arctica* (cf. VAN WINGERDEN, 1973).

During the winter period, especially when flooding of the lower parts of the beach plain occurs, the populations of *Hypogastrura viatica*, as well as of *Erigone arctica* are found mainly in higher patches of vegetation *(Agrostis stolonifera* and *Festuca rubra)* and at the basis of small dunes. Both species, occurring together in these areas, are involved then in relationships of other prey and predator species, which are living in this areas throughout the year. Preliminary observations indicate that the species, occurring in these areas, remain biologically active.

Thus during winter indirect relationships occurring on the basis of the distribution pattern of the species, lead to another type of direct relationships.

CONCLUSIONS AND DISCUSSION

It has been demonstrated that two, periodically interrelated types of relationships play a role in the investigated « community » of pioneer-organisms:

1. functional relationships (direct);
2. structural relationships (indirect).

The indirect relationships are favourable for *Hypogastrura viatica* during late spring and summer. At that time the same relationships are unfavourable for the main predator *Erigone arctica.*

During winter the relationship between the two species is affected by abiotic factors e.g. flooding, which cause changes in the pattern of distribution, and as a consequence both species are found at places where other prey and predator species occur.

It can be concluded that the pattern, as well as fluctuations in the pattern over the year are very important for the direct relationships of prey and predator species.

It should be remarked that these phenomena especially were investigated with respect to the edaphic fauna. Relationships within the bottomfauna as well as the aerial fauna were not, or only briefly, studied.

The species, which have been studied, to our opinion, could be named the « key-industries » in this community (cf. ELTON, 1927 and ELTON and MILLER, 1954). ELTON (1927) originally used this concept for herbivores (primary consumers) occurring in high densities. In our opinion the concept should be widened to those organisms, occurring in different trophic levels, which build up populations with high densities (according to the trophic level). They should be named « key-species ». The direct relationships of such species (populations) give the « skeleton » of such a community. The importance of such species should be evaluated not only in terms of abundance, but also in terms of energy-transport form one trophic level to another.

On the other hand it is shown in this study that indirect relationship should not be neglected. ELTON (1954) — again — has used the concept « girder-system » for this type of *interfering* activities of organisms in their

functional relationships, so that food-chains are connected. ELTON (1954) states: « the term « girder-system » (is) a metaphor that contains both a fact and a hypothesis: the fact that there are strong biotic links between different (gall) communities, and the hypothesis that such links may give strength to the whole interspersed population complex (in galls) ». TISCHLER (1973) studied such a « girder-system », starting from the role of *Angelica sylvestris* L. in an ecosystem. However, to our opinion it could be of interest to connect the interrelations he demonstrated, with the population dynamics of the (hibernating) species he studied.

We think that « key-species » and « girder-systems » should be studied on the basis of quantitative research on populations. Both the direct influences of « key-species » on each other and the influence of « girder-systems » (interfering organisms) should be continued in a developing « community » for some time. Changes which occur in both, if studied quantitatively, may give some more basic insight into the question « How operates a biocommunity ? »

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SUMMARY

Some species, occurring in a newly developing area, are studied in their direct and indirect relationships. Direct (functional) relationships (food) cannot be studied without knowledge about indirect (structural) relationships. The concepts of « key-species » and « girder-systems » in pioneer - communities are discussed. It is thought that by quantitative studies of the populations of key-species and their girder-systems these interrelationships can provide basic data in answering the question « How operates a biocommunity ? »

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